8.—The genus Morethia (Lacertilia, Scincidae) in Western Australia

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Manuscript received 21 March, 1972; accepted 18 July, 1972.

Abstract

The seven species and subspecies of Morethia occurring in Western Australia are described and keyed, viz. M. taeniopleura ruficauda (Lucas & Frost), M. taeniopleura exquisita subsp. nov., M. boulengeri (Ogilby), M. butleri (Storr), M. obscura sp. nov., M. lineoocellata (Dumeril & Bibron), and M. adelaidensis (Boulenger), Lectotypes are designated for Morethia anomalus Gray [= M. lineoocellata] and for Ablepharus lineoocellatus adelaidensis "Peters" |= M. adelaidensis (Boulenger)].

Introduction

Following Boulenger (1887) most authors have placed all the skinks with an immovable transparent eyelid in the genus *Ablepharus*. This reliance on a single character brought together species from different continents with little or nothing else in common (Fuhn 1969a), and it generically separated skinks that were very closely related (Greer 1967).

Fuhn (1969b) has shown that the Australian skinks with ablepharic eyes fall into about nine groups, including the genus *Morethia*. For the skull morphology of *Morethia* and other ablepharie skinks, the reader is referred to Dr. Fuhn's papers.

This revision of the western species of *Morethia* has been greatly aided by Dr. Miehael Smyth's concurrent study of the South Australian species, all of which extend into Western Australia. I am indebted to Mr. A. F. Stimson of the British Museum for the loan of type specimens.

Genus Morethia Gray

Morethia J. E. Gray 1845, "Catalogue of the specimens of lizard in the collection of the British Museum", p. 65,

Type-species (by monotypy).—Morethia anomala Gray (ibid.).

Diagnosis.—Small pentadactyl skinks with lower eyelid immovable and transparent; frontoparietals and interparietal normally fused into a single quadrilateral shield; supranasal and postnasal present (except in lineoocellata, where they are often fused to nasal). Distinguishable from Cryptoblepharus by frontal much larger than (rather than subequal with) prefrontals and by palpebral dise not completely surrounded by granules.

Distribution.—Throughout most of Australia.

Distribution.—Imoughout most of Australia

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Characters (additional to those in diagnosis).—Frontonasal in broad contact with rostral. Prefrontals usually separated, rarely forming a short suture. Frontal in contact with first 2 of 4 supraoculars. Usually one pair of nuchals. Ear lobules present (except in some races of taeniopleura), first (i.e. dorsalmost) usually largest. Upper labials normally 7, third-last largest and subocular.

Material.—M. t. taeniopleura (5 speeimens), t. ruficauda (40), t. exquisita (40), boulengeri (12), butleri (28), obscura (180), lineoocellata (115), adelaidensis (71). Apart from type material borrowed from the British Museum, all specimens cited in the text are in the Western Australian Museum.

Key

- No vertebral stripe; usually no ear lobules taeniopleura ruficauda
 A white vertebral stripe and small ear lobules usually present

taeniopleura exquisita

- 3. Subdigital lamellae obtusely keeled or smooth . .. 4
 Subdigital lamellae sharply keeled . 6
- 4. Fourth supraeiliary not smaller than third 5

 Fourth supraciliary much smaller than third ... boulengeri
- 5. Fifth supraeiliary (like third and fourth) penetrating deeply between supraoeulars; supranasal often fused to nasal; dorsal ocelli and midlateral white stripe usually well developed lincooeellata

Fifth supraeiliary not penetrating deeply between supraoculars; supranasal always separate from nasal; dorsal oeelli and midlateral white stripe absent or weakly developed obseura

6. Supraciliaries normally 6 and forming straight-sided series . . . butleri
Supraciliaries normally 5, last three penetrating deeply between supra-oeulars adelaidensis

Morethia taeniopleura ruficauda

Ablepharus lineo-ocellatus var. ruficaudus Lucas & Frost, 1895, Proc. Roy. Soc. Vic. (new ser.) 7: 269. Goyder River or Bagots Creek, Northern Territory (fide Coventry 1970: 119).

Diagnosis.—The species taeniopleura is distinguishable from other Morethio by its black or blackish, unspotted back and somewhat depressed head. The subspecies M, t, ruficauda is distinguishable from M, t, taeniopleura (Peters) of eastern Queensland by its four (rather than five) supraciliaries; subdigital lamellae obtusely keeled or narrowly callose (rather than smooth or broadly callose); and more strongly developed dorsolateral stripe

(silvery white, rather than pale brown; as wide or nearly as wide as pale midlateral stripe, rather than much narrower; and extending forward beyond supraciliaries).

Distribution.—Kimberley Division and north coast of North-West Division southwest to the De Grey. Extralimital in Northern Territory (except far north, where it is replaced by an undescribed race).

Description.—Snout-vent length (mm): 18-36 (30). Tail (% SVL): 128-189 (154).

Supranasal always and postnasal almost always present, though occasionally fused to each other or merely separated by a shallow groove.

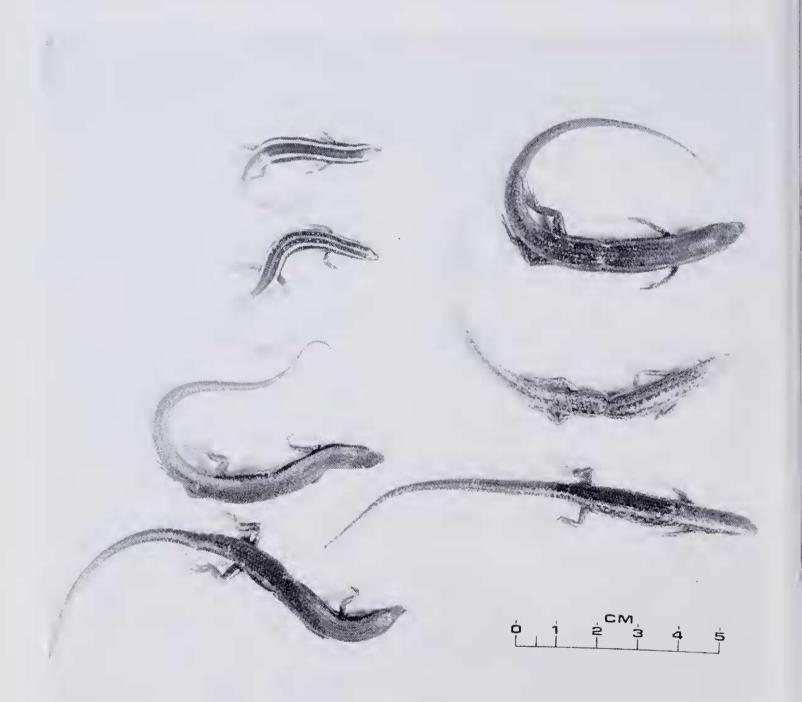


Figure 1.—Photograph of species and subspecies of Morethia occurring in Western Australia. Left, top to bottom: taeniopleura ruficauda, taeniopleura exquisita, boulengeri, and butleri. Rlght, top to bottom: obscura, lineoocellata, and adelaidensis.

Supraciliaries 4, second and third largest and penetrating deeply between supraoculars, third and forth forming a roughly linear junction with supraoculars. Ear lobules usually absent three specimens have 2 or 3 small obtuse lobules). Midbody scale rows 26-30 (mostly 26 or 28, mean 27.4). Lamellae under fourth toe 16-21 (mean 18.6), narrowly callose or obtusely keeled.

Head, back and sides glossy black. Tail red. White dorsolateral stripe often extending forward to snout and meeting its opposite number. White midlateral stripe narrowly or not edged below with black.

Material.—Kimberley Division (W.A.): Kalumburu (27972-8, 40497, 40951-6), Wotjulum (11213-7), Derby (20274~82, 20342), 12 mi. S of Derby (23009-10), Geikie Gorge (32153), Broome (27971, 40957), Frazier Downs (27965). North-West Division (W.A.): De Grey Station (2126). Northern Territory: Katherine (23162), Wauchope (34637), 26 mi. SW of Wauchope (24323), Dover Hills (40150).

Morethia taeniopleura exquisita subsp. nov. Holotype.—R 37709 in Western Australian Museum, collected by Mr. John Wombey on 16

September 1970 at Tambrey, Western Australia, in 21°37′S, 117°36′E,

Diagnosis.—Distinguishable from all other races of taeniopleura by whitish vertebral stripe.

Distribution,—North-West Division, from Depuch Island and Marble Bar, south to the Cape Range, the middle Gascoyne and the upper Ashburton.

Description.—Snout-vent length (mm): 15-45 (31). Tail (% SVL): 155-211 (190).

Supranasal and postnasal always present, though occasionally fused to each other. Supraciliaries normally 4, second and third largest and penetrating deeply between supraoculars, third and fourth forming a roughly linear junction with supraoculars. Ear lobules 0-4, small and obtuse, first usually largest. Midbody scale rows 26-32 (mostly 26 or 28, mean 27.2). Lamellae under fourth toe 17-24 (20.5), broadly callose to finely keeled.

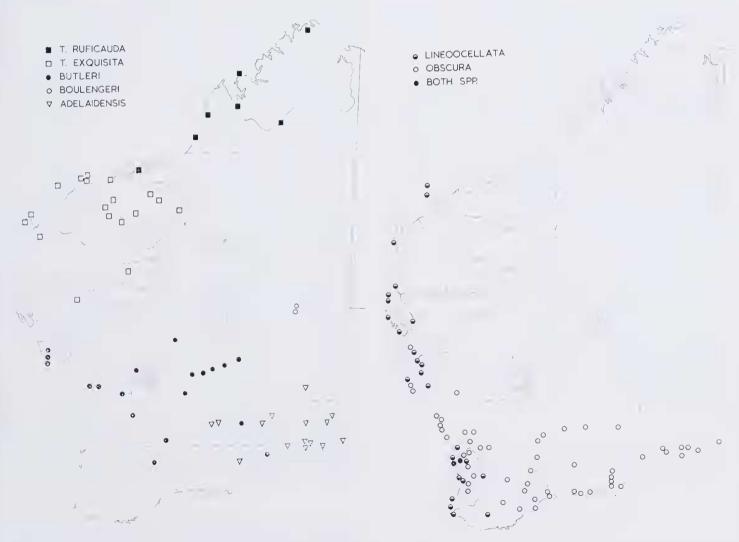


Figure 2.—Map of Western Australia showing location of specimens of Morethia taeniopleura, M. but'eri, M. boulengeri and M. adelaidensis. Drawn by Margaret H. Shepherd.

Figure 3.—Map of Western Australia showing location of specimens of Morethia lineoocellata and M. obscura. Drawn by Margaret H. Shepherd.

Coloration as in M, t, ruficauda with addition of greyish-white vertebral stripe.

Material.—North-West Division (W.A.): Marble Bar (18403-4); Mt Edgar (18398-402); Skull Springs, Davis River (39051); upper Cockeraga River (36595-6); 9 mi. S of Wittenoom (37088); Asbestos Creek (20015); upper Sherlock River (20014); Depuch Island (14574); Legendre Island (14332, 14360); Dolphin Island (14290-1, 14298, 37292-3); Rosemary Island (37393); Barrow Island (27966-70, 40689-91); Exmouth (31440); Shothole Canyon, Cape Range (18405); Yardie Creek (the watercourse, not the homestead) (21775); Marrilla (5338); Chalk Springs, Ethel River, 30 mi. SE of Mt Vernon (22799-800); Coordewandy (28383-5).

Morethia boulengeri

Ablepharus boulengeri J, D, Ogilby, 1890, Rec. Aust. Mus. 1; 10. Cootamundra, N.S.W. (H. J. McCooey). Diagnosis.—Six supraciliaries, first and third largest, last four forming a decreasing series, their junction with supraoculars roughly linear. Further distinguishable from M. butleri by smooth or obtusely keeled subdigital lamellae.

Distribution.—Far eastern interior of Western Australia (vicinity of Warburton Range), east through South Australia, New South Wales and south Queensland to the western slopes of the Great Dividing Range.

Description.—Snout-vent length (mm): 27-50 (40). Tail (% SVL): 137-177 (155).

Supranasal and postnasal always present but either fused to each other or merely separated by shallow groove. Ear lobules 2-4 (usually 2), usually obtuse. Midbody scale rows 30 or 32 (30.7). Lamellae under fourth toc 18-23 (20.0), broadly or narrowly callose.

Back olive green, variably marked with black (small spots or broken lines through middle of scales). Broad black upper lateral stripe. Moderately broad white midlateral stripe.

Remarks.—I am grateful to Dr M. Smyth for the two specimens from Salter Springs and for their identification with boulengeri, the type of which he has examined.

Material.—Eastern Division (W.A.): Warburton Mission (22016, 22110-1); Ainslie Gorge (18296). South Australia: 116 mi. N of Cook (36656); Emu (36612-3); Leigh Creek (40570); Salter Springs (39795-6). Queensland: Alum Rock, near Amiens (18545); Fernvale (18544).

Morethia butleri

Ablepharus butleri Storr, 1963, W. Aust. Nat, 9: 46. Leonora, W.A. (G. M. Storr & R. E. Moreau).

Diagnosis.—Supraciliaries 6 (rarely 7), first largest, remainder forming a decreasing series, their junction with supraoculars nearly linear. Further distinguishable from *M. boulengeri* by sharply keeled subdigital lamellae.

Distribution.—Arid and semiarid parts of southern interior of Western Australia, between

latitudes 27°30′ and 32°30′S, west to about the eastern edge of the Wheat Belt, and east to the western edge of the Great Victoria Desert and of the Nullarbor Plain.

Description.—Snout-vent length (mm): 25-56 (46). Tail (% SVL): 134-169 (152).

Supranasal and postnasal always present, though often fused to each other or merely separated by a shallow groove. Ear lobules 2-5 (mostly 2 or 3, mean 2.6). Midbody scale rows 26-31 (mostly 28 or 30, mean 28.9). Lamellae under fourth toe 19-27 (22.4).

Head and back dark olive-brown or olivegreen, usually unmarked, rarely flecked with black. Tail red in juveniles, brown in adults. Broad black upper lateral stripe and white midlateral stripe variably developed—prominent, indistinct, or absent except anteriorly. Lips dark-spotted.

Remarks.—In the far east of its range butleri approaches the closely related boulengeri in that the supraciliary-supraocular junction is not so linear, though it is the fourth (not the third) supraciliary that tends to protrude. Moreover, boulengeri in the far west of its range approaches butleri in the number and nature of subdigital lamellae, viz. 20-23 in the vicinity of Warburton Range, against 18-20 elsewhere, and here the subdigital calli are almost narrow enough to be called obtuse keels. However, it would be premature to treat these two skinks as races of one species. More needs to be learnt about their distribution in western South Australia, where Dr Smyth (pers. comm.) has examined a specimen of butleri from Ooldea, which is not far south and southeast of boulengeri localities.

Material.—South-West Division (W.A.): Lockwood Spring, Kalbarri National Park (37569); 19 mi. E of Kalbarri (33595); 26 mi. ESE of Kalbarri (33810); 7 mi. E of mouth of Hutt River (28003); 25 mi. E of Morawa (40958); Bonnie Rock (24872); Holt Rock (30941). Eastern Division (W.A.): Rothsay State Forest (29606); Youanmi (21164); Kathleen Valley (31672, 39697); Yamarna (18297, 20684); White Cliffs (20665-8); Laverton (18298); Mt Morgans (15686, 18339-44); Leonora (20615); Menzies (18324-5): 10 mi. E of Maroubra (34136); 29 mi. S of Karalee (36075); 12 mi. E of Zanthus (18307). Eucla Division (W.A.): 25 mi. W of Caiguna (24673).

Morethia obscura sp. nov.

Holotype.—R 16916 in Western Australian Museum, collected by Mr. John Dell on 7 November 1962 at 6 miles east of Kalamunda, Western Australia, in 31°58′S, 116°08′E.

Diagnosis.—Supraciliaries 6 (rarely 5), fourth largest, last three forming a decreasing series, their junction with supraoculars roughly linear. Otherwise generally similar to *M. lineoocellata* and differing only in greater size, darker coloration, less distinct pattern, and invariable presence of supranasal.

Distribution.—Southern Western Australia: north on west coast to a little beyond the Murchison; east on south coast to Eucla; inland to Morawa, Wongan Hills, Tammin, Coolgardie and Zanthus; also many islands off lower west coast from Gun Island (Houtman Abrolhos) to Garden Island (off Fremantle). Apparently absent from far southwest, i.e. south of Bunbury and west of Albany. Extralimital in southern South Australia.

Description.—Snout-vent length (mm): 18-56 (43). Tail (%SVL): 126-189 (152).

Supranasal and postnasal always present, though often fused to each other or merely separated by a shallow groove. Ear lobules 1-4 (2.3). Midbody scale rows 24-30 (mostly 26 or 28, mean 27.0). Lamellae under fourth toe 17-23 (19.3), smooth or obtusely keeled.

Upper surface dark olive-grey or olive-brown. Back with or without small, usually indistinct, black-and-white ocelli or black flecks. Rarely any indication of a pale dorsolateral line. Broad black upper lateral stripe variably developed. Pale midlateral stripe usually absent or poorly developed (i.e. narrow, ragged-edged and suffused with grey).

Material.—South-West Division (W.A.): Zuitdorp Cliffs, 40 mi. N of Kalbarri (18597); Morawa (34004); Gun Island, Houtman Abrolhos (27190-2); No. 5 Island, S of Gun Island (30436); Pelsart Island, Houtman Abrolhos (27142, 27161-70, 30438-9); Fisherman Island (18386-93, 39954); Long Island, Jurien Bay (18381); Escape Island, Jurien Bay (17889); 4 mi. E of Jurien Bay (30505); Cervantes Island (18384-5); Buller Island (19154); Green Islets (18382-3); 15 mi, N of Lancelin (18396); Lancelin Island (18384-5); 7 mi. N of New Norcia (26051); Wongan Hills (4238); 8 mi. W of Bolgart (40959); Tammin (39087); Meekering (21748); Chidlows (21345); 6 mi. E of Kalamunda (16917, 19248, 19829, 22260-1, 34713, 39690); Wanneroo (14863, 34053); Crawley (18321-3); Spearwood (2768); Carnae Island (7255, 11995); Garden Island (13024, 18373-8, 35036-41); Cannington (18320); Glen-(32471); Boddington (13560); Samson Brook Dam (18329); 5 mi, SW of Collie (18317); 10 mi. N of Tarin Rock (40051-3, 40096); Lake Varley (25988); 26 mi. SE of Newdegate (21736); Lake Magenta (21737); Jerramungup (18318); Toolbrunup (1385); Two People Bay (18293-4); Cheyne Beach (36040, 36016); Chillinup (26685); Bremer Bay (33402-4); Fitzgerald River Reserve (36946, 36995, 37200, 37210); Hopetoun (11010); 10 mi, N of Hopetoun (36249). Eastern Division (W.A.): 17 mi. S of Karalee (33991); 13 mi. W of Boorabbin (40512-4); Coolgardie (18295); 30 mi. E of Kalgoorlie (7070, 12228); 18 mi. E of Zanthus (12236). Eucla Division (W.A.): Mt. Holland (33990); Daniell (30785); 22 mi. N of Esperance (18292); Dalyup River (18289-90); Shark Lake (18291); Esperance (10235-6, 11369, 11782, 13397); 23 mi. E of Esperance (18288); Israelite Bay (18286, 33402-4); 4 mi. S of Mt Ragged (17617); Junana Rock (17608-10); Pine Hill (17600-2, 22519, 36220-2); Coragina Rock (17473, 18287, 36182); 25 mi. W of Caiguna 24674-5); 4-15 mi. SE of Cocklebiddy (24658-62, 31890-1, 34471-5, 34486, 34551-2); Madura (26436); 27 mi. S of Madura (34442-4); 22 mi. E of Madura (36660); 20 mi. S of Mundrabilla (26435); Eucla (24618-9, 31874). South Australia: 4 mi. E of Wilsons Bluff (28131): Ceduna (24568-9); Smoky Bay (24556-62); 17 mi. W of Port Lincoln (27365).

Morethia lineoocellata

Ablepharus lineo-ocellatus A. M. C. Duméril & G. Bibron, 1839, "Erpétologie générale" 5: 817. New Holland.

Morethia anomalus J. E. Gray, 1845, "Catalogue ... specimens ... lizard ... British Museum", p. 65. Western Australia (John Gilbert).

Diagnosis.—Supraeiliaries 6 (oceasionally 5, owing to fusion of first and second), third, fourth and fifth equal in size and penetrating deeply between supraoculars. Otherwise generally similar to M, obscura and differing only in lesser size, paler and brighter coloration, more conspicuous pattern (especially strong development of midlateral stripe and dorsal occili), and tendency for supranasal to fuse with nasal.

Distribution.—Midwest eoast of Western Australia from Point Cloates south to Geraldton, and on islands from the Montebellos south to the Houtman Abrolhos; inland as far as Mt. Curious. Lower west coast of Western Australia from a little north of Perth south to Cape Leeuwin; also on islands (Rottnest and Garden) and sporadically inland as far as Canning Dam, Mooterdine and Rocky Gully.

Description.—Snout-vent length (mm): 19-49 (35). Tail (% SV): 111-247 (172).

Supranasal usually fused to nasal or merely separated by a shallow or incomplete groove. Postnasal usually present, though usually separated from nasal by only a faint groove. Ear lobules 1-3 (1.8). Midbody scale rows 24-31 (mostly 26 in south and 28 in north, mean 27.3). Lamellae under fourth toe 16-26 (19.7), smooth or obtusely keeled.

Head coppery brown. Back green, olive-grey or olive-brown, usually marked with black and white ocelli. Ocelli oceasionally absent or modified into black and/or white spots which may coalesee into longitudinal lines. White dorso-lateral line variable in development—often indistinct or absent. White midlateral stripe usually well developed and margined with black.

Remarks.—I have examined Gray's syntypes and have chosen one of them (British Museum 1946.8.15.75) as lectotype of Morethia anomalus.

Material.—North-West Division (W.A.); Trimouille Island (37464); Barrow Island (28674); Point Cloates and Ningaloo (13185, 16860-1); 11 mi. SE of Ningaloo (16977-81); 24 mi. N of Carnarvon (18328); Bernier Island (11253, 13188-91, 20516-23, 34089); Dorre Island (13186-7); Dirk Hartog Island (12474); Gladstone (18330); Carrarang (39030). South-West Division (W.A.);

Gee Gie Outcamp, 21 mi. NNW of Murchison House (34037); Mt. Curious (33440); Murchison House (29923): Kalbarri National Park (37615, 37635); Lockwood Spring, 20 mi. E of Kalbarri (33476-8); 19 mi. NNW of Ajana (33665); 25 mi. W of Ajana (29625); Port Gregory (18326); East Wallabi Island, Houtman Abrolhos (18394-5); 4 mi. S of Geraldton (18327); 12 mi. W of Muchea (12702); Morley Park (32370); Rottnest Island (2015-6, 2560, 2861-3, 2994-6, 11009, 12750-1, 12758-61, 13770, 13797, 15201-2, 17130, 18345-72, 36156); Bentley (29654, 32383); Applecross (21606); Spearwood (2769); Garden Island (28475-7); Point Peron (18319); Canning Dam (26483); Mooterdine (40960-1); Lake Clifton Wagerup (6491); Dunsborough (18310-6): (18308); Cowaramup (13734); Margaret River (7960-1); Karridale (27959-64); Rocky Gully

Morethia adelaidensis

Ablepharus lineo-ocellatus var. adelaidensis "Peters", Boulenger, 1887, "Catalogue . . . lizards , . . British Museum (Natural History)" 3: 349. South Australia (Gerard Krefft).

Diagnosis.—Supraciliaries normally 5, last three largest and penetrating deeply between supraoculars; subdigital lamellae sharply keeled; ground colour slightly rufescent; pale midlateral stripe wavy-edged.

Distribution.—Arid southeast of Western Australia (Nullarbor Plain and vicinity), north nearly to latitude 29°S and west nearly to Kalgoorlie. Extralimital in South Australia.

Description. — Snout-vent length (mm): 17.5-53 (42). Tail (% SVL): 125-172 (153).

Supranasal and postnasal invariably present but often fused to each other or merely separated by a shallow groove. Ear lobules usually hidden by projecting pre-auriculars; occasionally 1-3 visible. Midbody scale rows 26-31 (mostly 28 or 30, mean 28.9). Lamellae under fourth toe 17-23 (19.8).

Dorsally olive-brown or olive-grey, variably tinged with rufons brown. Small black spots on back tending to form broken paravertebral lines. Pale dorsolateral stripe occasionally discernible on body, reappearing above eye as well-defined curving line. Broad, dark brown upper lateral stripe ill defined. Whitish midlateral stripe usually margined below with dark brown. Under digits rufous brown.

Remarks.—Boulenger (supra cit.) ascribed the name adelaidensis to Peters. In the cited place (Mber, Preuss. Akad. Wiss. 1874: 375-6) Peters described Ablepharus (Morethia) taeniopleurus, which he briefly compared with "Ablepharus (Morethia) anomalus (adelaidensis)". This passing mention of adelaidensis does not constitute a valid description. Nor do I believe it was Peters' intention to introduce a new name here; I think this was simply his way of referring to

Adelaide specimens of what he took to be Ablepharus anomalus.

I therefore regard Boulenger as the authority for the name *adelaidensis*. According to Dr Smyth (pers. comm.) the specimens of "adelaidensis" listed by Boulenger actually comprise two species. In order to stabilise the name, I have examined Boulenger's two South Australian specimens and have chosen one of them (British Museum 64.10.27.9) as lectotype of *Morethia adelaidensis* (Boulenger).

Material,—Eastern Division (W.A.); Randalls (18299-300); Karonie (14234-8); Narctha (18301-6, 39712-3); 100 mi. N of Loongana (29459). Eucla Division (W.A.); Seemore Downs (18331-8); Loongana (29430-1, 34502, 37671); Forrest (15817); 18 mi. NE of Forrest (15180); Eucla (24620-3); Mundrabilla (11001, 25470); Madura (25471); 20 mi. N and 24 mi. NE of Madura (29417-22, 36166-7); Cocklebiddy (36554-5); 12 mi. SW and 14 mi. S of Balladonia (17386, 17417, 17419-20). South Australia; Koomooloobooka Cave (25416-21); Pidinga (25422-4, 25428, 25469); Ceduna (25551); 6 mi. N of Kokatha (24506-9); Wingfield (39793-4).

Discussion

As in some other widespread but small genera. e.g. Nephrurus and Tympanoeryptis, the various species of Morethia tend to have mutually exclusive ranges. In the Kimberley and Northwest Divisions there is only taeniopleura. The arid and semiarid country further south is oceupled by butleri, which itself is replaced in the far east of the State by the closely related boulengeri. The ranges of the three species occurring in the south of the State, lineooccillata, obscura and adelaidensis, are respectively centred on the west-coastal plain, the precambrian shield, and the halophytic country of the southeast. However, obseura has invaded the coastal plain in several places; it is also marginally sympatric with the southernmost populations of butleri and adelaidensis,

The fact that *Morethia* species are largely allopatric would suggest that they have evolved in situ; or in other words their ranges are much the same as when they were geographic races of a single widespread species. This might be taken as evidence that the various species are young, or have evolved too recently for their ranges to have changed much. Such a view would be supported by the great similarity in scalation between the species, only the supraciliaries showing any substantial differentiation. Moreover the relationship of obscura to lineoocellata and of boulengeri to butleri must be very close.

Nevertheless I cannot believe that the radiation of *Morethia* is very recent. The differences in coloration between, say, *taeniopleura*, *lineoocellata* and *adelaidensis* are marked and manifold, and are in no degree bridged by geographic or individual variants. Moreover the genus itself is probably old. With its persistent

supranasals and postnasals, *Morethia* stands apart from other endemic Australian genera of skinks; at the same time it is not clearly related to any non-Australian genus.

One is thus left with the probability that the restricted ranges of *Morethia* species are due to ecological factors rather than lack of time for expansion. Each species, it seems, is so well adapted to a given climate-substrate type that its congeners are at a disadvantage within its range. In *Nephrurus* and *Tympanocryptis*, where interspecific differences in morphology are more trenchant, the case for invoking ecological factors is still more cogent.

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